POLSKA AKADEMIA NAUK
INSTYTUT ZOOLOGICZNY, ODDZIAŁ W KRAKOWIE

ACTA ZOOLOGICA CRACOVIENSIA

Tom I Kraków, 15 IX 1956 Nr 1

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Studia nad morfologią pancerza żółwi współczesnych i kopalnych. I—II

Исследования по морфологии панцыря современных и ископаемых черепах. I—II

Studies on the morphology of the shell of recent and fossil tortoises. I—II

[Pl. I—II and 1 text-figure]

I

SYMMETRICAL AND REGULAR ANOMALIES IN THE STRUCTURE OF THE SHIELDS OF THE SHELL

In 1946 the former Natural History Museum of the Polish Academy of Science (now Institute of Zoology of the Polish Academy of Science, Branch in Kraków) received a small collection of reptiles and amphibians from the Near East. In this collection there are several specimens of tortoises, one of which, *Testudo graeca ibera* Pallas [Pl. I, fig. 1, 2] deserves particular attention. J. J. Sagan, member of the staff of the Institute, collected this specimen in Irak, not far from Khanaquin, in summer, 1941. The external characters of the specimen show that it is a rather small, adult female. A particular feature of this specimen is the presence of elongated marginal shields, on both sides of the carapace, caused by the fusion of five marginal shields, namely those from IV to VIII (the so-called scuta margino-lateralia, Schreiber, 1912, p. 753). The furrows, normally separating these shields, are in

this case not at all impressed on the surface of the plates of the shell. The shape of these large, abnormal shields is very regular and their position, in relation to the main plane of symmetry of the animal's body, is exceptionally symmetrical. For this very reason the shields do not impress one, at the first sight, as a distinct anomaly in the structure of the shell. Apart from that, anomalies in the structure of shields — of an asymmetric and irregular character — which are so often found in tortoises, occur in this specimen too. Thus, the individual concerned has only three vertebral shields on the right side of the carapace (I to III) and although four shields are present on the left side (I to IV), the shields III and IV are distinctly narrow and are built abnormally. In the bridge region the surface of the shields is crossed by furrows forming irregular zigzags. These are „vestigial" furrows of the marginal shields IV—VIII. Apart from the mentioned deviations from the general type of shell structure, the individual shows no differences in comparison with other specimens of the species *Testudo graeca* LINNÉ s. lat.

Deviations and anomalies in the structure of the tortoise shell have been often described and figured by many authors. This peculiar inclination of tortoises was already well known to BOJANUS (1819/1921, pl. II). In his classical work on the anatomy of the European pond tortoise he gave figures of carapaces showing distinctly asymmetrical and irregular structures of shields and plates.

Similar anomalies of the shields and plates of the carapace were described by the known paleontologist H. v. MEYER (1865/68) in the fossil land tortoise *Testudo antiqua* BRONN and in the recent European pond tortoise. Other, undoubtedly interesting examples of deviations in the structure of the tortoise shell, were given by COOKER (1910), VOGEL (1912), SCHREITMÜLLER (1930), GLAESSNER (1926) and others.

Cases of deviations and of all sorts of variations of a regular and symmetrical character — similar to the case described above — are relatively rare.

Already COKER (1910) stated that the „asymmetry" in the structure of the horny shields can go such different ways that sometimes the shields may secondarily become even symmetrical.

According to DERANIYAGALA (1930, 1934) the number of costal shields of the disc in the common sea turtle *Caretta caretta* (LINNÉ) is very often increased, and is usually more than four, and sometimes even as large as ten. Since this increase in the number of shields occurs, in principle, on both sides of the carapace and is symmetrical, one is not aware of a distinct irregularity. In connection with this, the mentioned author suggests that in the ancestors of this turtle the definitive hardening of the corselet following the hypothetical evolutionary „armadillo“ stage, occurred still before the definitive and final reduction of the primary costal shields, that is earlier than in any other species. This undoubtedly original and interesting explanation offered by DERANIYAGALA (1930) has not found, unfortunately, sufficient paleontological and morphological support, and the author's hypothesis concerning the existence of an evolutionary „armadillo“ stage, in which the hypothetical „*Protestudinata*“ were able to coil, has not been sufficiently proved.

Symmetrical and regular anomalies in the structure of shields of tortoise shells have been observed and described several times in fossil forms. Probably the first case of this sort was described by H. v. MEYER (1856/58) in the new species „*Emys*“ *turnauensis* H. v. MEYER [1], which he established. In the specimen, described by this author, the anterior costal shields were eliminated and replaced totally by the excessively widened and enlarged anterior vertebral shields. These morphological features are regarded by the author as important specific characters. His opinion, concerning the matter, is explained as follows (op. c., p. 52): „Der Verlauf der Grenzeindrücke ist in dieser Schildkröte so regelmässig, dass der Mangel an Seitenschuppen unmöglich für eine zufällige Erscheinung oder für eine Abnormalität gehalten worden kann, er wird der Spezies wirklich zugestanden haben und es wird sich eigentlich nur um Entscheidung der Frage handeln, ob der gänzliche Mangel einer Schuppenart in einer Schidkröte zur Errichtung eines eigenen Genus berechtigt, oder nur zu dem Kennzeichen gehört, welche bei der Unterscheidung von Spezies in Anwen-

[1] According to E. FUCHS (1938) this species belongs to the genus *Clemmys* RIDGEN and not to *Emys* DUMÉRIL.

dung kommen". The above quotation shows clearly that the author's argumentation was strongly influenced by the regularity in the shape and in the distribution of the shields of the shell.

A very similar case of incorrect determination of a fossil tortoise is found in the rather well known work by BODA (1927) [Fig. 1A]. This author described a new genus and species under the

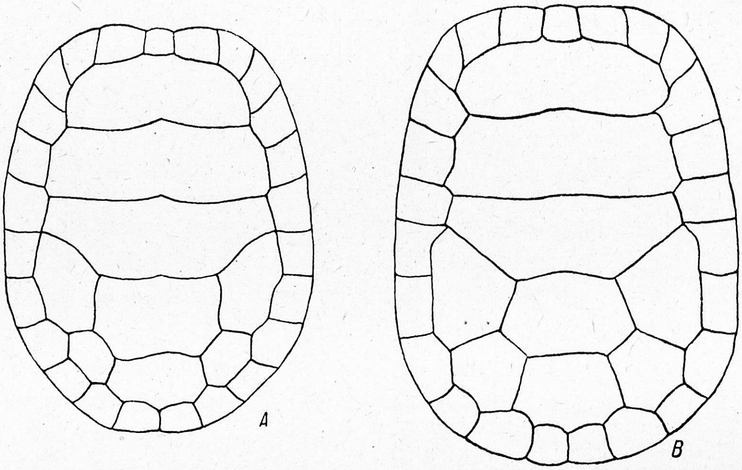


Fig. 1. A. Schematic drawing of the carapace of *Geomyda sopronensis* BODA; after BODA (1927). B. Schematic drawing of the carapace of *Clemmys steinheimiensis* STAESCHE; after STAESCHE (1931/1934). Visible large vertebral shields in the cranial part of both tortoises, which replaced completely the adjoining costal shields.

name „*Clemmydopsis*" *sopronensis* BODA from Lower Pannonian horizons near Sopron in Hungary. The descriptions, as well as the carefully done drawings and photos, show that in the discussed specimen the costal shields I and II are completely eliminated and replaced by the vertebral shields I, II and III in the cranial part of the carapace. The schematic drawing, given by BODA, shows that the vertebral shields and the small costal shields, in the posterior (caudal) part of the carapace of the tortoise from Sopron, have very regular outlines and are all placed symmetrically in relation to the main plane of symmetry of the animal's body. It was this regularity and

symmetry of the shields on which the author based the description of the „new" genus. Giving arguments in support of his view BODA (op. c.) referred the above quotation from the paper of H. v. MEYER (op. c.).

According to SZALAI (1930, p. 356) the establishment of the new genus by BODA was unfounded, since in this case wehave to do with a distinct anomaly and deviation from the general type of shield structure occurring sporadically in various species of tortoises. SZALAI (l. c.) thinks moreover that „*Clemmydopsis*" has morphological characters (the shape of the neural plates) analogous to those of the recent East Asiatic species *Geoemyda trijuga thermalis* (LESSON); thus he holds the name of the genus „*Clemmydopsis*" BODA for a synonym of the genus *Geoemyda* GRAY (in SZALAI's nomenclature *Nicoria* GRAY [1]. In the Tertiary, the tortoises belonging to the above genus occurred in Europe in several localities.

STAESCHE (1933) had to do with a very similar case. The shape of the anterior vertebral shields and the lack of costal shields, eliminated by the former, were to him the basis for the description of a new species form the „Steinheimer Becken" (upper Miocene, Germany), named *Clemmys steinheimensis* STAESCHE [Fig. 1B]. Just like the previously quoted authors he considers the shape and the composition of the shields of the carapace as taxonomically important characters justifying the description of a new species. Explaining his point of view STAESCHE (op. c.) refers mainly to the publication of BODA (op. c.), quoted in the present paper.

In 1938 appeared the work of E. FUCHS (1938) in which the author described the remnants of a fossil tortoise under the name *Clemmys turnauensis* (H. v. MEYER) from the Miocene brown coal horizons in Oberpfalz (Germany). The first vertebral shield of the tortoise, described by the author, is distinctly widened and the first pair of costal shields is reduced, just as it was in the type of H. v. MEYER (op. c.). We can see, that anomalies of this kind occur relatively frequently in fossil Emydins.

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[1] The present name of the genus, *Geoemyda* GRAY, was used by SZALAI (1932, p. 2).

Descriptions of new forms, based on the appearance and the shape of some regular shields of the shell, normally not to be found in tortoises, were done as well in the case of recent species. A similar mistake to those made by the authors mentioned above was made by the eminent herpetologist F. WERNER (1899, p. 818, quoted after SIEBENROCK, 1906, p. 84). This author described namely a new variety of *Testudo hermanni* GMELIN [in WERNER's work (l. c.) *Testudo graeca* LINNÉ] „from the vicinity of Trebinje in Bosnia", under the name „*hercegoviensis*" WERNER. According to WERNER, this new variety differed from the typical form of *Testudo hermanni* GMELIN, by the presence of additional crescent-shaped shields, formed through the division of the abdominal shields by additional furrows, the latter being branches of the medial furrow and terminating at the place where they meet the pectoral-abdominal furrow. According to SIEBENROCK (1906) this variety was described on the basis of characters which can appear sporadically in specimens of this species. SIEBENROCK noticed similar shields not only in specimens from Herzegovina but also in those from Albania (Scutari). In addition, SIEBENROCK (op. c.) studied the occurrence of these morphological characters in a large material from various parts of the Balkan Peninsula and he came to the conclusion that the occurrence of additional shields on the s c u t a a b d o m i n a l i a is not an essential, real taxonomical characters; it is merely an individual and anomalous feature, transmitted, may be, to the offsprings of a „hereditarily affected" pair of parents („Daraus dürfte wohl zu Genüge hervorgehen, dass man es hier nicht mit einem konstanten Merkmal zu tun habe, sondern mit einer individuellen Anomalie, die sich möglicherweise von einem damit behafteten Elternpaar auf die Nachkommen vererbt hat"). We can assume that one of the reasons why WERNER (op. c.) describedt hat „new" variety was probably the symmetry and the regularity in the structure of these additional shields of the plastron.

These few examples, mentioned above, show clearly that regular and symmetrical variations in the shield structure of the tortoise shell can be erroneously taken for characters of a new form — a genus, species or subspecies. Deviations of this kind are particularly dangerous to specialists working

on fossil or subfossil forms, since the material at their disposal is scanty and very often extremely fragmentary.

Thus, we should never overestimate such morphological details as the shape, the lack or the presence of the shields of the shell in establishing a new species or subspecies. At the same time we should remember that particularly all chelonogical papers must be based on the largest possible comparative material.

II

TAXONOMIC VALUE OF THE SUPRAPYGAL PLATES IN THE GENUS *TESTUDO* LINNÉ.

The presence of one or two suprapygal plates (suprapygalia sive postneuralia sive supracaudalia, nec scuta!) is usually considered as one of particularly important taxonomic characters in determining the species of land tortoised of the genus *Testudo* LINNÉ.

According to SIEBENROCK (1915) all Palaearctic species, belonging to the mentioned genus, have as a rule one suprapygal plate [in SIEBENROCK's work (op. c., p. 359) — supracaudale]. These are: *Testudo hermanni* GMELIN (SIEBENROCK — *T. graeca* L.), *T. marginata* SCHOEPFF, *T. graeca* L. (op. cit. *T. ibera* PALLAS), *T. horsfieldi* GRAY and *T. kleinmanni* LORTET. According to SIEBENROCK, the South African species, *T. oculifera* KUHL, should be added to these Palaearctic species from the shores of the Mediterranean.

The following species of the genus *Testudo* LINNÉ have two suprapygal plates: *T. denticulata* LINNÉ, *T. sulcata* MILLER, *T. chilensis* GRAY, *T. emys* SCHL. & MÜLL., *T. pardalis* BELL, *T. elegans* SCHOEPFF, *T. geometrica* LINNÉ, *T. radiata* SHAW, and three giant turtles from oceanic islands belonging to the group of *T. elephantopus* HARLAN. The author thinks that other giant turtles have also two suprapygal plates. Yet, according to SIEBENROCK (op. c.) the presence of one or two suprapygal plates in not an absolutely constant character. The author himself found several times the presence of two suprapygal plates in the Palaearctic species *T. graeca* LINNÉ (*T. ibera* PALLAS). The suprapygal plate of this species is often divided by a transversal suture into two parts. A similar

specimen of this species is found in the comparative anatomical collection of the Institute of Zoology of the Polish Academy of Science, Branch in Kraków. The shell of this tortoise comes from the vicinity of Khanaquin in Irak. The anterior (cranial) part of the pygal plate of this individual is divided by a suture, the latter bending arc-like toward the caudal margin of plate one.

According to Siebenrock (op. c.), the number of suprapygal plates is probably always constant in two other Palaearctic species, *T. hermanni* Gmelin, and *T. marginata* Schoepff. It appears, however, that specimens of one of the mentioned species may have sometimes two suprapygal plates. In the tortoise collection of the Institute of Zoology of the Polish Academy of Science in Warszawa is a shell of a large male of *Testudo marginata* Schoepff (inv. No. 2303), which has two distinct suprapygal plates [Pl. II, fig. 3]. Unfortunately it is not known exactly where the specimen comes from. The shape of the suprapygal plate one resembles that of an equilateral triangle the top of which, cut off and rounded, is directed toward the cranium. This plate is surrounded by the sides of the suprapygal plate two, thus being isolated from the costal plates and from the last neural plate (neurale 8). The shape of the second suprapygal plate resembles that of the letter V turned upside down. It must be stressed that both plates are placed distinctly symmetrically to each other and their margins have a very regular outline; thus, the whole pygal region of the carapace gives no impression of any anomaly in structure. Siebenrock (op. c.) found quite a similar position and shape of the plates in question in two specimens of *T. graeca* Linné from Macedonia. The well known fossil species *Testudo kalksburgensis* Toula, has an identical type of suprapygal plates. This tortoise was described for the first time by Toula (1896) from the upper Miocene in Austria. Other Tertiary species, for instance *Testudo syrmiensis* Koch, described from the Pannonian horizons in Croatia (Koch, 1904), have also two suprapygal plates. It is quite probable, that the latter name is a synonym of *T. kalksburgensis* Toula, since both species are extremely similar. It is rather significant that *T. kalksburgensis* Toula resembles very closely still another

known Tertiary species, *Testudo antiqua* Bronn. The only essential character distinguishing these two species is just the presence of those two remarkable suprapygal plates in *T. kalksburgensis* Toula, the plates being similar to analogous plates found in the specimen of *T. marginata* Schoepff, described and figured above. The shells of *T. kalksburgensis* Toula and *T. antiqua* Bronn closely resemble those of recent Palaearctic species of the group „*graeca*", and first of all of the subspecies *Testudo graeca graeca* Linné. Differences between these two tortoises are more of a rather quantitative (in German „graduelle") than qualitative nature (e. g. carapace more strongly and distinctly vaulted, thicker plates etc.). Thus, *Testudo antiqua* Bronn, having one suprapygal plate, may be considered most probably as the ancestor of the recent species *T. graeca* Linné s. lat. One should mention here the fact, that Glaessner (1933) does not recognize *T. kalksburgensis* Toula as a separate species (he always puts the name of the species in quotation marks); he considers the name to be a synonym of certain forms belonging to the group „*antiqua-graeca*", which he himself has established. For some strange reasons Glaessner's statement is based on the supposition that both *T. antiqua* Bronn and *T. kalksburgensis* Toula have always two distinct suprapygal plates of the same type as the plates described in the present paper (Glaessner, op. c., p. 362).

Since the wrongness of this view was already demonstrated by Szalai (1935) there is no reason to go back to this matter. In view of the facts, described in the present paper and referring to sporadical, individual occurrence of two suprapygal plates in contemporary Palaearctic species, we may ask whether *T. kalksburgensis* Toula is not merely an anomalous, individually changed specimen of the species *T. antiqua* Bronn.

The very close resemblance of these two tortoises makes one think that this may be the case. The examples, quoted above, point to the conclusion, that two suprapygal plates may occur sporadically in various representatives of the Palaearctic group „*graeca*". This character occurs particularly often in the recent species *T. graeca* Linné. If we consider the fact that this species is very similar to its probable fossil ancestor

T. antiqua Bronn, we may very well suppose that specimens of the latter species could have had exceptionally two suprapygal plates also. In this case, the real existence of a distinct species *T. kalksburgensis* Toula, based first of all on the discussed anatomical character, seems very problematic.

All forms possessing two suprapygal plates, described by Toula (1896), Staesche (1931) or Koch (1904) should be treated as individual variations of specimens of the species *T. antiqua* Bronn s. lat. It is also not quite improbable that in the Tertiary the same territory in Europe was inhabited by two very similar species, differing in the structure of the pygal region of the carapace in a similar way as the recent South African species *T. oculifera* Kuhl and *T. radiata* Shaw. In such a case, the close resemblance of both fossil species in question would be of a convergent character.

In order to prove one of the two possibilities — whether *T. kalksburgensis* Toula should be treated as a separate species or as a case of individual variation within the species *T. antiqua* Bronn — we have to study the occurrence of the discussed character in a large material, coming from various places. Unfortunately, such numerous finds are rare and the existing fossil species, possessing two suprapygal plates, have been described on the base of scanty material. In this case a larger number of caudal parts of the carapace is most important and not fragments of shells and skeletons of these tortoises in general. Until more numerous fragments of pygal parts of shells belonging to one of the mentioned species have been found in one locality and in the same horizon, the problem concerning the real existence of the species *T. kalksburgensis* Toula has unfortunately to remain unsettled.

The examples quoted above point to the conclusion that the number of suprapygal plates, and even their morphology are not a reliable taxonomical character allowing to determine quite precisely to what species belongs a given tortoise of the genus *Testudo* Linné. The morphology of the pygal region may have great taxonomic value only when large comparative material has been studied. Since in the case of fossil tortoises this large material is not available, we should look for other, more reliable taxonomic characters. It seems, however, very

doubtful whether in the case of tortoises, animals of such exceptionally variable morphological features, one „reliable“ and „unfailing“ specific character can be singled out. Thus, all fossil and recent species should be determined only on the base of the whole complex of their morphological characters.

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STRESZCZENIE

I

SYMETRYCZNE I REGULARNE NIEPRAWIDŁOWOŚCI W BUDOWIE TARCZEK ROGOWYCH PANCERZA

Notatka niniejsza zawiera krótki opis odchyleń w budowie tarczek rogowych pancerza lądowego żółwia *Testudo graeca ibera* Pallas pochodzącego z Iraku z okolic Khanaquin. U osobnika tego po obydwóch stronach karapaksu występują duże, długie tarczki brzeżne (scuta margino-lateralia) powstałe przez stopienie się ze sobą tarczek brzeżnych od IV do VIII. Powyższe odchylenie ma charakter wyjątkowo symetryczny, a kształt tarczek jest bardzo regularny.

Oprócz tego u opisanego okazu możemy stwierdzić częste u żółwi nieprawidłowości w budowie tarczek pancerza o charakterze niesymetrycznym.

W dalszej części omówiono kilka podobnych przykładów odchyleń w budowie i układzie tarczek rogowych występujących u gatunków współczesnych i kopalnych. Tego rodzaju anomalie w budowie tarczek pancerza były często powodem tworzenia przez autorów „nowych" rodzajów czy gatunków.

II
ZNACZENIE TAKSONOMICZNE PŁYTEK SUPRAPYGALNYCH (SUPRAPYGALIA) W RODZAJU *TESTUDO* LINNÉ

Autor podaje krótki opis dodatkowej płytki suprapygale 2 występującej w karapaksie żółwia lądowego *Testudo marginata* SCHOEPFF. Na podstawie sporadycznego występowania dwóch płytek suprapygalnych u niektórych osobników należących do palearktycznej grupy „*graeca*", autor przypuszcza, że z tym samym zjawiskiem możemy mieć do czynienia w przypadku form kopalnych z tzw. grupy „*antiqua-graeca*" (GLAESSNER, 1933). W takim przypadku kopalny gatunek *Testudo kalksburgensis* TOULA charakteryzujący się obecnością dwóch płytek suprapygalnych mógłby być indywidualnie zmienionym osobnikiem z gatunku *Testudo antiqua* BRONN charakteryzującego się obecnością jednej płytki suprapygalnej. Nie jest jednak wykluczone, że podobne dwa gatunki o jednej i o dwóch płytkach suprapygalnych żyły obok siebie na tym samym terytorium i w tym samym czasie, a ich wzajemne podobieństwo ma charakter konwergencyjny. Bliższe udowodnienie jednego z tych przypuszczeń będzie wtedy dopiero możliwe, gdy zostanie znaleziony znacznie liczniejszy materiał kopalny.

РЕЗЮМЕ

I
СИММЕТРИЧЕСКИЕ И ПРАВИЛЬНЫЕ УКЛОНЕНИЯ В СТРОЕНИИ РОГОВЫХ ЩИТКОВ ПАНЦЫРЯ

Настоящая заметка дает краткое описание уклонений в строении роговых щитков панцыря наземной черепахи *Testudo graeca ibera* PALLAS происходящей из Ирака, из окрестностей Ханекина. У этого экземпляра на обеих сторонах карапакса находятся большие, удлиненные маргино-латеральные щитки (scuta margino-lateralia) образовавшиеся путем слияния друг с другом маргинальных щитков от IV до VIII. Это уклонение отличается исключительно симметрическим характером, и форма щитков очень правильна.

Кроме того у описываемого экземпляра можно было найти частые у черепах уклонения в строении щитков панцыря несимметрического характера.

В дальнейшем описано несколько аналогических примеров уклонений в строении и расположении роговых щитков у современных и ископаемых видов. Такого рода аномалии в строении щитков панцыря часто были причиной создавания некоторыми авторами „новых“ видов и даже родов.

II
ТАКСОНОМИЧЕСКОЕ ЗНАЧЕНИЕ СУПРАПИГАЛЬНЫХ ПЛАСТИНОК (SUPRAPYGALIA) В РОДЕ *TESTUDO* LINNÉ

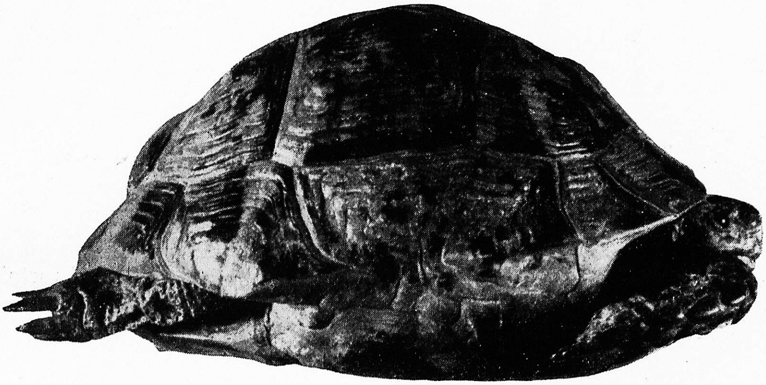
Автор дает краткое описание добавочной пластинки suprapygale 2 в карапаксе наземной черепахи *Testudo marginata* SCHOEPFF. На основании спорадически встречающихся двух супрапигальных пластинок у некоторых экземпляров принадлежащих к палеарктической группе „*graeca*“ автор предполагает, что мы можем иметь дело с аналогическим явлением у ископаемых форм из так называемой группы „*antigua-graeca*“ (GLAESSNER, 1933). В таком случае ископаемый вид *Testudo kalksburgensis* TOULA, характеризирующийся наличьем двух супрапигальных пластинок, мог бы быть индивидуально видоизмененным экземпляром вида *Testudo antiqua* BRONN имеющего одну супрапигальную пластинку. Однако не исключено, что два сходных вида с одной и с двумя супрапигальными пластинками жили рядом одновременно на том же ареале, а их взаимное сходство является конвергентного характера. Более точно, доказать одно из этих предположений будет возможно только, когда будет собран гораздо более многочисленный ископаемый материал.

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Plate I

Fig. 1. Photograph of the left side of *Testudo graeca ibera* PALLAS, Marginal shields seen in the pictures show an exceptionally symetrical position.

Fig. 2. Photograph of the right side of *Testudo graeca ibera* PALLAS.



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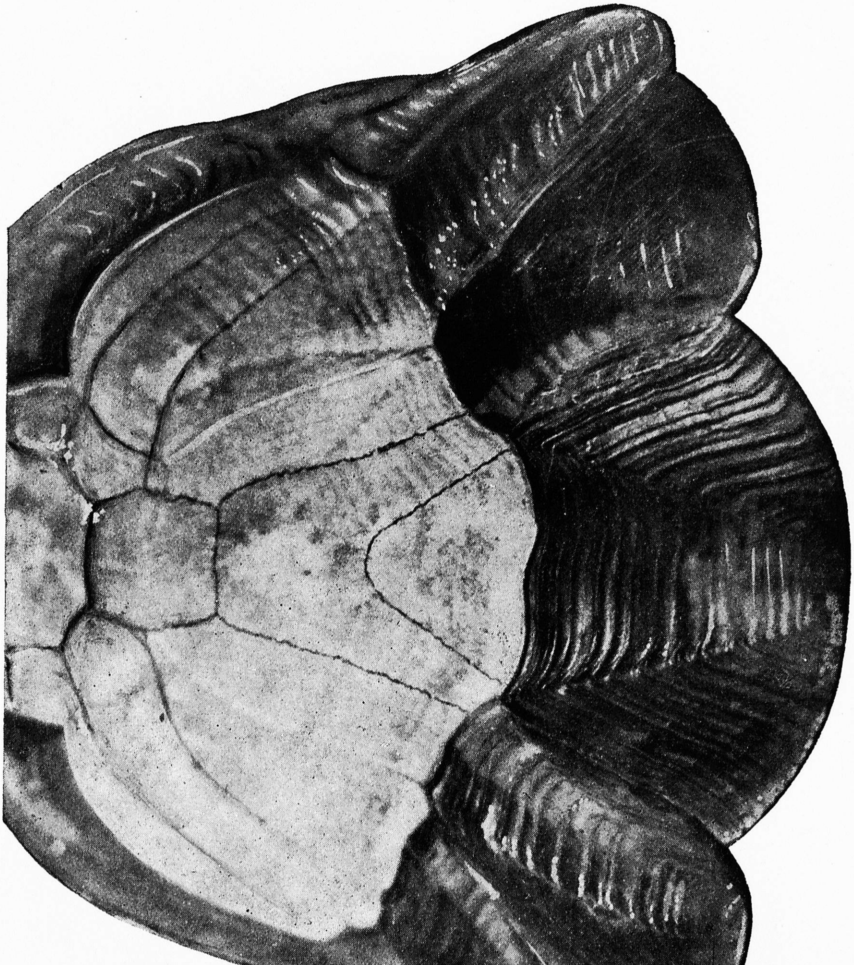


2

A. Pigoń phot.
M. Młynarski

Plate II

Fig. 3. Photograph of the pygal region of the carapace of the land tortoise *Testudo marginata* SCHOEPFF. The sutures of the plates were retouched on the specimen with India ink.



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S. Myczkowski phot.
M. Młynarski

Redaktor pracy—prof. dr T. Jaczewski

Państwowe Wydawnictwo Naukowe — Oddział w Krakowie 1956

Nakład 1370+135 egz., Ark. wyd. 1, druk. 1+4 tabl. Papier ilustrac. kl. III g 80, 70×100 cm
Nr zam. 151/56 M-7-15999 Cena 2.— zł

Krakowska Drukarnia Naukowa